The Evolution of Dispersal in Reserve Networks

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abstract: The fragmentation of an environment into developed and protected areas may influence selection pressure on dispersal by increasing the chance of moving from a favorable to an unfavorable habitat. We theoretically explore this possibility through two cases: (1) marine systems in which reduced predation and/or increased feeding drive the evolution of planktonic larval duration and (2) more generally, where stochasticity in reproductive yield drives the evolution of the proportion of offspring dispersing. Model results indicate that habitat fragmentation generally shifts selection pressure toward reduced dispersal, particularly when areas outside reserves are uninhabitable. However, shifts to increased dispersal may occur when temporal heterogeneity is the primary selective force and constant-quota harvest occurs outside reserves. In addition, model results suggest the potential for changes in the genetic variability in dispersal after habitat fragmentation. The predicted evolutionary changes in dispersal will depend on factors such as the relative genetic and environmental contributions to dispersal-related traits and the extent of anthropogenic impacts outside reserves. If the predicted evolutionary changes are biologically attainable, they may suggest altering current guidelines for the appropriate size and spacing of marine reserves necessary to achieve conservation and fisheries goals.

Keywords: evolution of dispersal, habitat fragmentation, reserves, Marine Protected Areas, game theory.

By substantially changing ecological and evolutionary landscapes, anthropogenic effects significantly alter selection pressure and can cause rapid evolution on ecological timescales (Palumbi 2001; Ashley et al. 2003; Stockwell et al. 2003). One common way in which humans are altering environments is by fragmenting them into protected areas such as reserves surrounded by developed or exploited areas (Vitousek et al. 1997). Because reserves better protect shorter-distance dispersers that are more likely to stay within reserve boundaries, such habitat fragmentation may alter selection on dispersal distances (Allison et al. 1998; Botsford et al. 2001).

Specifically, while stochastic (temporal) environmental heterogeneity tends to shift selection pressure toward greater dispersal (e.g., more dispersing offspring) in models of the evolution of dispersal (e.g., Levin et al. 1984), static spatial heterogeneity tends to shift selection pressure toward reduced dispersal due to the increased chance of movement from a favorable to an unfavorable habitat (e.g., Hastings 1983; reviewed by Johnson and Gaines 1990). Therefore, since it imposes static spatial heterogeneity, habitat fragmentation is likely to shift selection pressure toward reduced dispersal. Providing theoretical support for this expectation, habitat loss and fragmentation lead to the evolution of lower dispersal rates and distances in both general simulations and simulations specific to marine species with planktonic larvae (Travis and Dytham 1999; Dytham 2003; Parvinen 2004; but see Heino and Hanski 2001).

The effect of fragmentation on the evolution of dispersal is particularly relevant in the context of marine reserves compared to terrestrial reserves because of the generally greater potential for dispersal across all levels of marine ecosystems (Carr et al. 2003). For example, estimates from multiple types of data suggest that the maximum dispersal scale of sedentary marine species with planktonic larvae is at least an order of magnitude greater than that of their terrestrial counterparts, plants with seed dispersal (Kinlan and Gaines 2003). Overall, much of this greater dispersal potential is due to the planktonic larval stage of many marine organisms (Carr et al. 2003).

In marine organisms with a planktonic larval stage, habitat fragmentation affects processes important to the evolution of dispersal. For example, because environmental heterogeneity influences the evolution of dispersal, anthropogenic habitat degradation, including changing the

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spatial pattern of heterogeneity with habitat fragmentation, alters the selection pressures acting on dispersal (Pechenik 1999). In addition, fragmentation into a reserve network affects how the number of settling offspring per adult depends on dispersal distance; this reproductive capacity is a frequently used measure of fitness in models of the evolution of dispersal for benthic marine species with planktonic larvae (e.g., Vance 1973; Christiansen and Fenchel 1979; Caswell 1981; Perron and Carrier 1981; Grant 1983; McEdward 1997; Levitan 2000).

Empirically, dispersal rates and distances have evolved, in some cases rapidly, in response to habitat fragmentation and anthropogenic impacts. For example, within several decades of anthropogenic introduction, cane toad leg morphology may have evolved to enhance dispersal at the invasion front (Phillips et al. 2006). In addition, reduced dispersal ability naturally evolves in isolated habitats; flightlessness in birds has repeatedly evolved on oceanic islands, possibly on the timescale of generations (McNab 1994), and reduced seed dispersal in wind-dispersed biennial plants may evolve on oceanic islands within a decade (Cody and Overton 1996). With respect to marine organisms, the number of gastropod species without planktotrophic larval development has increased over geologic time in the Gulf of Mexico, possibly due to isolation events associated with sea level changes (Hansen 1982). By isolating protected populations, anthropogenic habitat fragmentation may cause similar and perhaps rapid evolution of reduced dispersal.

Here we explore theoretically whether and how much the fragmentation of a habitat into protected and unprotected areas will affect the evolution of dispersal. Our assumption is that dispersal evolves in an undisturbed habitat due to natural selective forces, and we explore the effect of incorporating anthropogenic habitat fragmentation in a suite of models. Reserve network establishment often comes after anthropogenic disturbances impact populations through harvesting or habitat destruction (e.g., bottom trawling or coastal development affecting marine systems). However, we focus on the effect of reserves because reserve network design parameters such as size and spacing are the primary management tools available to control the impact of anthropogenic disturbance on the evolution of dispersal.

Natural selection on dispersal, including planktonic marine dispersal, may depend on a large variety of factors ranging from reduced kin competition to increased egg production (Crisp 1976; Strathmann 1985; Hedgecock 1986; Roughgarden 1989; Johnson and Gaines 1990; Pechenik 1999). In this article, we focus on two such factors based on our interest in marine systems: the case of "predictable variation" and the case of "unpredictable variation." First, in the predictable variation case, specific to coastal marine ecosystems, we assume that planktonic larval dispersal evolves as the byproduct of an adaptation to have a pelagic feeding period and/or to avoid benthic predation. In support of this hypothesis, larval dispersal tends to occur on a different spatial scale than one would expect if it were a direct adaptation to increase the probability of arriving at more suitable habitats; pelagic development may allow more access to food than benthic development, and the greater predator abundance in nearshore environments suggests that predation may be greater for benthically developing larvae (Strathmann et al. 2002).

Second, in the unpredictable variation case, applicable to both marine and terrestrial systems, we assume that dispersal evolves as a direct adaptation to stochastic environmental heterogeneity. We explore this case because reserve establishment directly affects the primary selective force by changing the spatial pattern of the environmental heterogeneity. While the factors modeled in the predictable and unpredictable cases interact in reality, this approach allows exploration of how the impact of fragmentation and reserve network design depends on the primary natural selective forces acting on the evolution of dispersal.

Models and Results

Model Overview

Before presenting the mathematical details, here we provide a conceptual overview of the models and analyses. First, the predictable variation case focuses on the evolution of initial larval size, which is critical to the evolution of dispersal in marine species with planktonic larvae. Generally, species with longer pelagic larval periods disperse farther (Shanks et al. 2003; Purcell et al. 2006) because of the greater amount of time spent as a primarily passive propagule experiencing processes such as advection and diffusion in coastal oceans. In addition, smaller eggs require longer pelagic periods (Levitan 2000), potentially because of the greater amount of time necessary to feed and grow to the settlement size.

For the predictable variation models, we define a species' population dynamics in terms of its initial larval size(s). For example, we assume fecundity decreases as initial larval size increases in a classic offspring size-number life-history trade-off. Because the smaller, more numerous larvae require a longer planktotrophic period to grow to the metamorphosis developmental stage, this trade-off incorporates the potential for the selective advantage of a pelagic feeding period to increase selection for planktonic dispersal. In addition, we explore two approaches to determine how larval survival depends on initial larval size. In the first approach, we divide the larval period into a lecithotrophic benthic stage (yolk-feeding larvae attached to the substrate

and thus not dispersing) and a planktotrophic pelagic stage (plankton-feeding oceanic propagules), with different mortality rates in each stage. In the second approach, we assume a general size-dependent larval mortality function. In both approaches, we assume the average dispersal distance increases with decreasing larval size (increasing pelagic duration). Finally, we assume that settlement and postlarval survival do not directly depend on the initial larval size; postlarval survival depends on location, with lower survival outside reserves than inside reserves due to constant-effort harvest.

In order to analytically explore the predictable variation case, we make two key assumptions; we assume that areas outside reserves are uninhabitable and that the population is evenly distributed in space. Under these assumptions, the predicted evolutionary outcome is the initial larval size that maximizes fitness, defined as the product of fecundity; larval survival; and retention within the reserve network (fig. 1). Fragmenting a pristine habitat into protected and unprotected areas increases the initial larval size (decreases the dispersal distance) that maximizes fitness (figs. 2, 3). In addition to providing a numerical example of the fitness function dependent on reserve network design (fig. 4), we determine the predicted evolutionary outcome in numerical simulations that relax the above assumptions (fig. 5). The simulations indicate that the predicted shifts in selection toward larger initial larval size (shorter dispersal distance) with fragmentation require greatly reduced postlarval survival in areas outside reserves.

Second, the unpredictable variation case focuses on the proportion of offspring dispersing as the evolving trait, where any dispersal is global (equally likely to end up in any location in the modeled region; fig. 6). In the context of marine systems, nondispersing offspring may represent benthically developing larvae and dispersing offspring may represent pelagically developing larvae. Survival differs for dispersers and nondispersers; disperser survival may be relatively lower if dispersal is costly or relatively greater if, for example, benthic larvae experience more predation than pelagic larvae. To model temporal variability in the environment, we focus on temporally heterogeneous reproductive yield because productivity, and therefore reproductive output, is highly variable in marine systems (Morgan 2001). In particular, the productivity is a random variable that can take on one of two values in each site and at each time step. In addition, we explore the reproductive yield dynamics with and without site saturation at settlement. Finally, we explore two approaches for the dynamics in the nonreserve sites: (1) constant-quota harvest

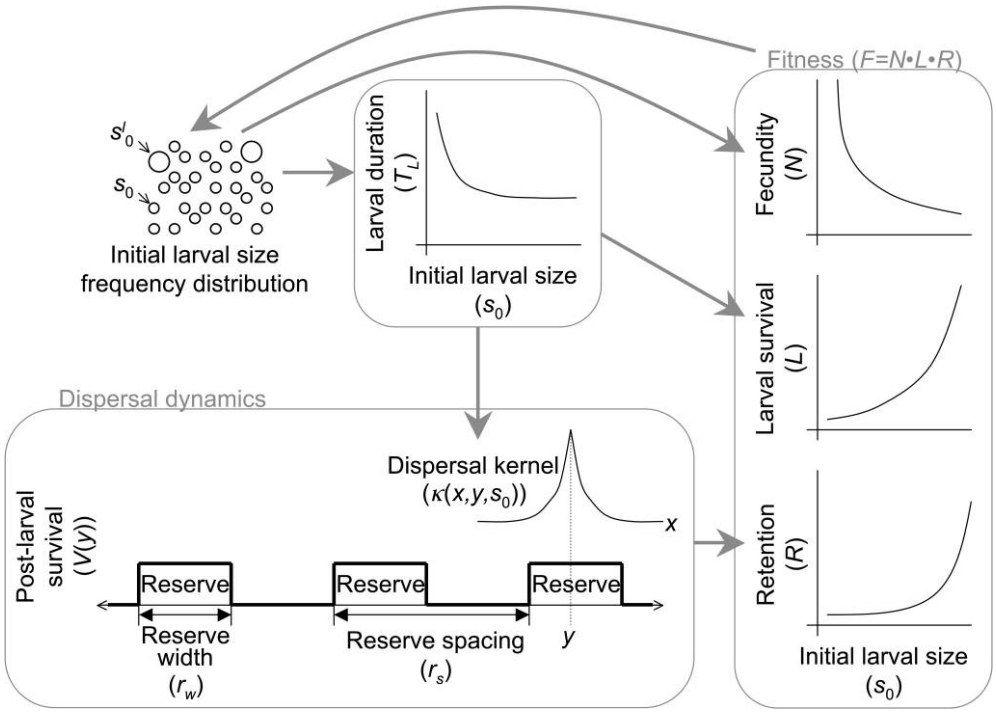

Figure 1: Outline of the case 1 (predictable variation) models, where benthic predation avoidance and/or planktonic feeding are the primary selective force(s) acting on the evolution of dispersal (eqq. [1]–[8]).

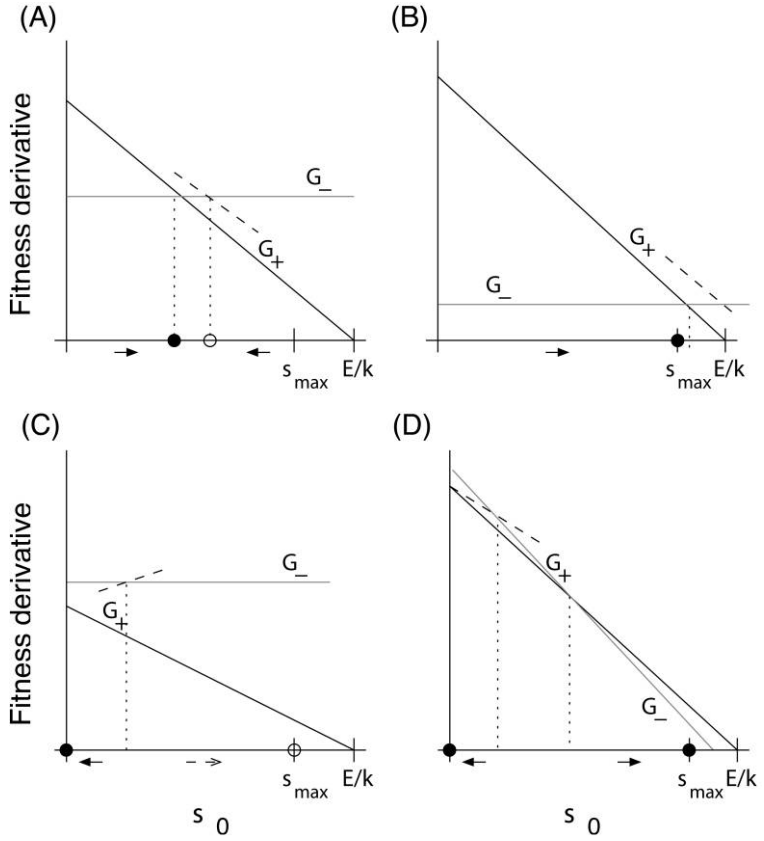

Figure 2: Potential outcomes for the case 1 (predictable variation) model with differential mortality in the pelagic and benthic larval stages. Solid gray lines are the negative component of the fitness derivative (eq. [A3]), solid black lines are the positive component of the fitness derivative in a pristine environment (eq. [A2]), and dashed black lines indicate the effect of adding fragmentation into a reserve network on the positive component. Filled circles indicate larval strategies (initial larval size s_0) that locally maximize fitness, and open circles indicate changes, if any, to the strategies that maximize fitness after fragmentation into a reserve network. Solid arrows indicate the direction of selection, and the dashed arrow indicates change to the direction of selection, if any. *A–D* show the different possible outcomes, depending on parameter values, for the larval strategies that locally maximize fitness.

lowers productivity outside reserves and (2) areas outside reserves are uninhabitable.

We analytically determine the range of possible evolutionary outcomes (fig. 7) and numerically explore representative cases of the potential outcomes (fig. 8). Because the primary natural selective force acting on dispersal is the productivity ratio of good to bad years and that ratio is greater in constant-quota harvested areas, decreasing reserve size shifts selection toward increased proportion of offspring dispersing. In addition, the different selection pressures within reserves and harvested areas may lead to increased variability in dispersal. However, when areas outside reserves are uninhabitable, decreasing reserve size shifts selection toward decreased proportion of offspring dispersing, without the potential for shifts in selection toward increased variability in dispersal. Preliminary simulations with localized (rather than global) dispersal provide analogous results (fig. 9).

In both the predictable variation and unpredictable variation cases, the dynamics explored are discrete-time models with one dispersal event per generation. Such models are most relevant to intensively harvested benthic marine invertebrates (e.g., abalone, urchins) and fish with relatively sessile adults (e.g., those that tend to have restricted home ranges). Marine reserves are likely to be a more effective management tool for such less mobile species due to the greater potential to protect the entire nonlarval component of their life cycles (Allison et al. 1998).

Finally, we use a game-theoretic approach throughout to develop general predictions, given the limited mechanistic knowledge about the genetics of dispersal-related traits (Havenhand 1995). In this approach, a dispersal "strategy"

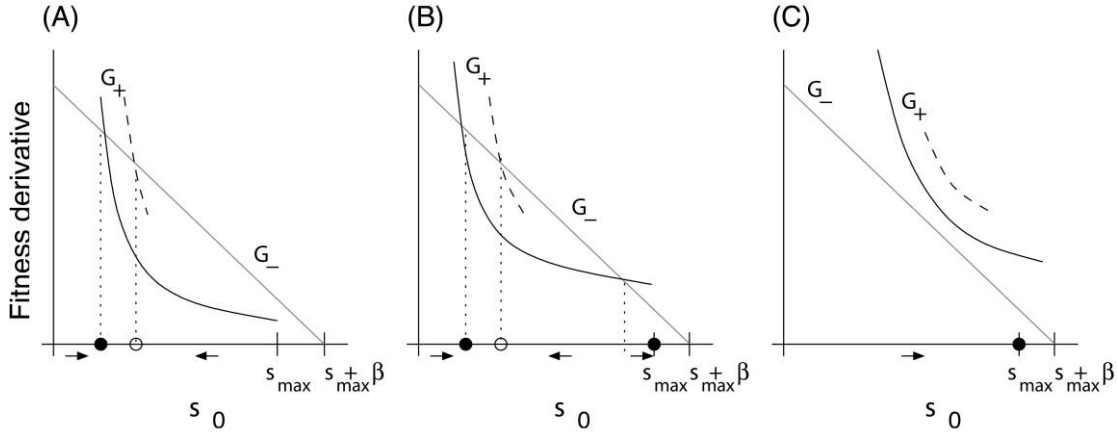

Figure 3: Potential outcomes for the case 1 (predictable variation) model with size-dependent larval mortality. Gray lines are the negative component of the fitness derivative (eq. [A6]), solid black lines are the positive component of the fitness derivative in a pristine environment (eq. [A5]), and dashed black lines indicate the effect of adding fragmentation into a reserve network on the positive component. Filled circles indicate larval strategies (initial larval size s_0) that locally maximize fitness, and open circles indicate changes, if any, to the strategies that maximize fitness after fragmentation into a reserve network. Solid arrows indicate the direction of selection. *A–C* show the different possible outcomes, depending on parameter values, for the larval strategies that locally maximize fitness. Adapted from figure 5 of Christiansen and Fenchel (1979).

denotes a phenotype, either initial larval size or proportion of offspring dispersing, linked to reproduction and survival. We search for dispersal strategies that cannot be invaded by any other strategies, or global evolutionarily stable strategies (ESSs; Maynard Smith and Price 1973), as well as strategies that can invade all other strategies, or global neighborhood invader strategies (NISs; Apaloo 1997). A strategy that is both an ESS and an NIS is an evolutionarily stable neighborhood invader strategy (ESNIS; Apaloo 1997). Note that the definition of an ESNIS is narrower than that of convergence stability (Christiansen 1991) because an ESNIS excludes both non-NIS and non-ESS convergence stable strategies (the latter of which are evolutionary branching points). Determining the global ESNIS indicates the likely evolutionary outcome because successive invasions by alternative strategies converge to the ESNIS strategy, which is then uninvadable by other strategies.

Case 1: Predictable Variation and the Evolution of Initial Larval Size

The evolution of initial larval size based on life-history trade-offs in benthic marine invertebrates with planktonic larvae has been extensively explored (reviewed by Havenhand [1995]). Here we present a game-theoretic framework where initial larval size is the focal strategy, which we extend to incorporate the effect of habitat fragmentation into a reserve network.

Case 1 Model Definition. To determine the initial larval size that is the ESNIS, we describe the population dynamics as a function of larval size (fig. 1). Let $n_t(x, s_0^i)$ be the number of individuals with initial larval size s_0^i at time t and location x on a linear coastline. Varying with initial larval size, the fecundity is $N(s_0^i)$, and the larval survival is $L(s_0^i)$. The postlarval survival $V(x)$ is independent of larval size but depends on the location x (protected or harvested areas). In addition, we assume that larval production is high enough to saturate each location x at settlement and that any density dependence affects all larval strategies equally. Therefore, settlement occurs in proportion to the frequency of each larval type $(n_t(y, s_0^i)/\sum_j n_t(y, s_0^j)$, where $\sum_j$ is the sum over all of the strategies in the population). In support of these assumptions, initial larval size primarily affects early larval stages in sea urchins and has little effect on late larval stages (Sinervo and McEdward 1988). Finally, $\kappa(x, y, s_0^i)$ is the dispersal kernel for larval strategy s_0^i with release location y and settlement location x. Taking the population census just after the dispersal stage of the life cycle, the basic model is

$$n_{t+1}(x, s_0^i) = \int_{-\infty}^{\infty} \kappa(x, y, s_0^i) L(s_0^i) N(s_0^i) V(y) \frac{n_t(y, s_0^i)}{\sum_j n_t(y, s_0^j)}\, dy. \tag{1}$$

In order to analytically explore whether a rare strategy s_0' will invade a population comprising the dominant strat-

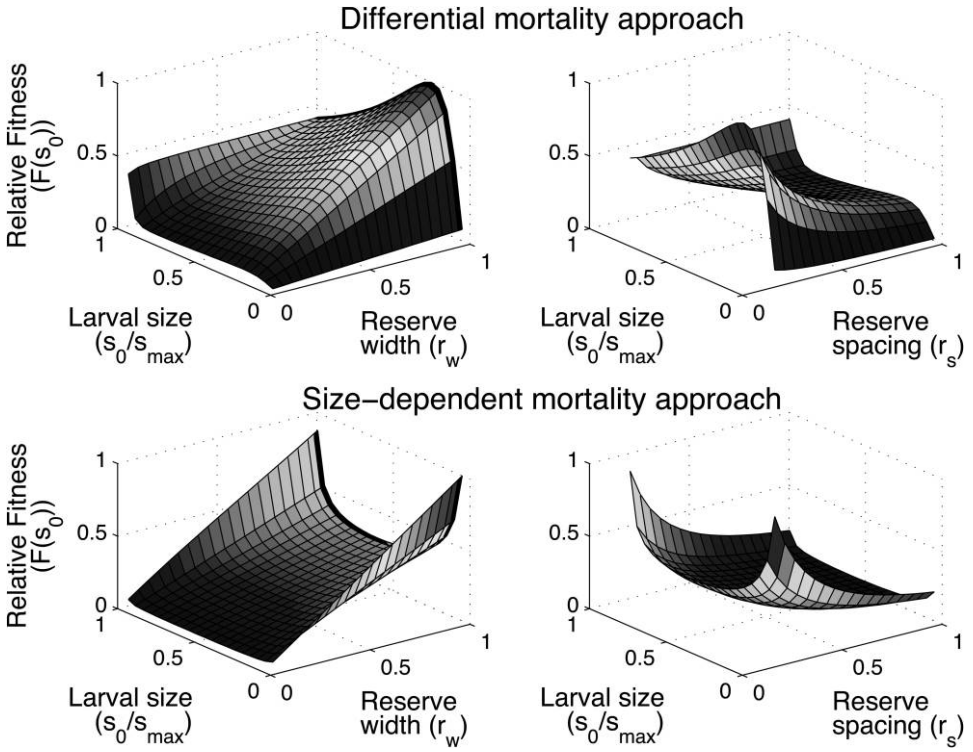

Figure 4: Example of the impact of reserve design on the fitness function for the case 1 (predictable variation) models: fitness (eq. [3]; relative to the maximum fitness for each plot) as a function of initial larval size (relative to maximum larval size s_{max}) and reserve width (proportion of region with one reserve; *left column*) or reserve spacing (proportion of region with 20% protected in total; *right column*). The approach with differential benthic and pelagic mortality (eqq. [4], [5]) is in the top row, and the approach with size-dependent mortality (eqq. [6], [7]) is in the bottom row. The black lines in the left-hand plots represent the fitness function in a pristine environment, previously explored by Christiansen and Fenchel (1979), Levitan (2000), Perron and Carrier (1981), and Vance (1973). See table 1 for parameter values. The initial larval size that globally maximizes fitness for a particular reserve width or spacing is the global evolutionarily stable neighborhood invader strategy.

egy s_0, we make a series of simplifying assumptions that we later relax in the numerical exploration. First we assume that areas outside reserves are uninhabitable; that is, $V(x) = 0$ for x in harvested areas, and $V(x) = v$ for x in the reserve network, which we represent with Ω. Next we assume that the population of each larval strategy is evenly distributed in space (i.e., ignore edge effects), where the population size at each point in space is approximately the average population size, represented by $\bar{n}_t(s_0^i) = (1/|\Omega|)\int_\Omega n_t(x, s_0^i)dx$. In addition, we define the larval strategy-dependent retention within the reserve network as $R(s_0^i) = (1/|\Omega|)\int_\Omega\int_\Omega \kappa(x, y, s_0^i)dydx$, analogous to the "average dispersal success" approach proposed by Fagan and Lutscherb (2006). With these assumptions and definitions, equation (1) becomes

$$\bar{n}_{t+1}(s_0^i) = R(s_0^i)L(s_0^i)N(s_0^i)v\frac{\bar{n}_t(s_0^i)}{\sum_j \bar{n}_t(s_0^j)}. \quad (2)$$

Given the above assumptions, a rare strategy s_0' will increase in frequency given dominant strategy s_0 if $F(s_0') > F(s_0)$, and it will decrease in frequency if $F(s_0') < F(s_0)$, where

$$F(s_0) = R(s_0)L(s_0)N(s_0) \quad (3)$$

(fig. 1). Thus, the initial larval size s_0^* that maximizes $F(s_0)$ is the stable strategy because it can invade all other strategies and is uninvadable. Note that this mean field approach causes the predicted evolutionary outcome to become independent of the frequency of other strategies; we test the importance of the mean field approximation and frequency dependence in spatially explicit numerical simulations. This fitness function $F(s_0)$ of an initial larval size s_0 is the reproductive efficiency, that is, the number of settled larvae per adult. Previous analyses of this type of model have explored the larval size that maximizes fitness in a pristine environment (e.g., Vance 1973; Christiansen and Fenchel 1979; Perron and Carrier 1981; Levitan 2000). We extend these models by incorporating the

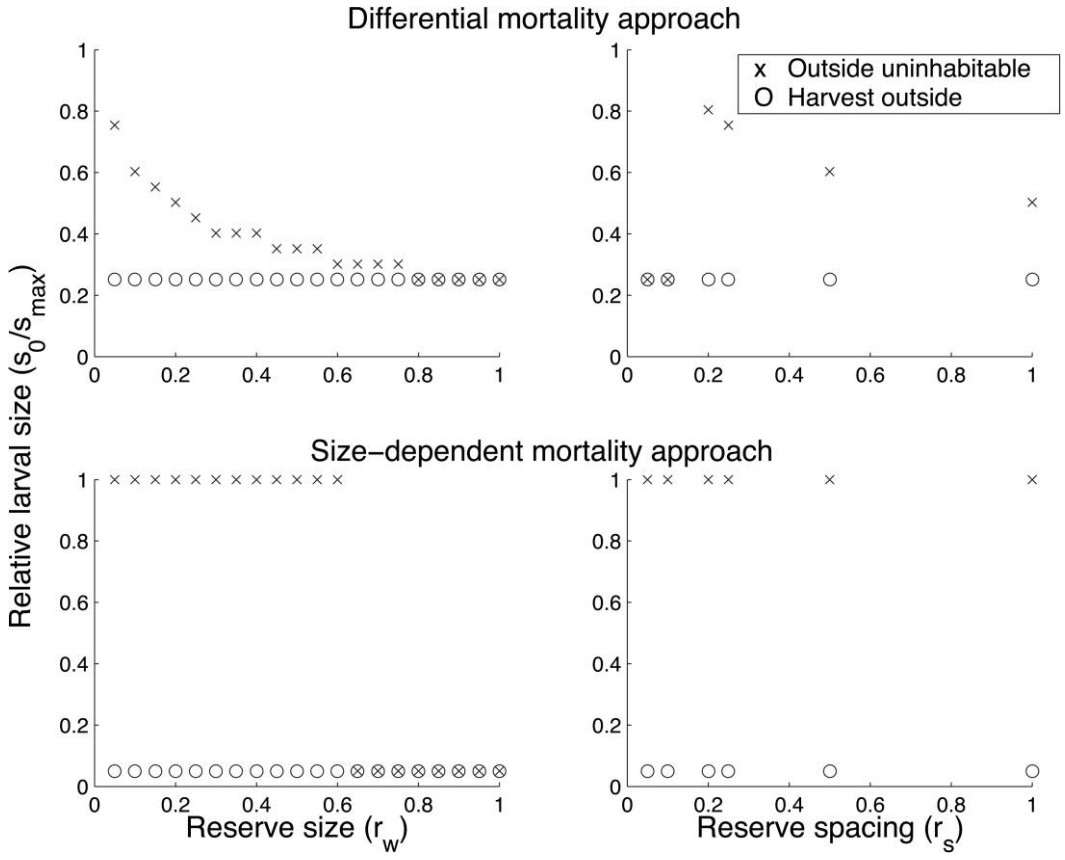

Figure 5: Numerical prediction of the initial larval size that is the global evolutionarily stable neighborhood invader strategy (ESNIS) for the case 1 (predictable variation) models (eq. [10]): ESNIS s_0^* (relative to the maximum larval size s_{max}) with varying reserve size (proportion of region with one reserve; *left column*) and spacing (proportion of region with 20% of the region protected in total; *right column*). The approach with differential benthic and pelagic mortality (eqq. [4], [5]) is in the first row, and the approach with size-dependent mortality (eqq. [6], [7]) is in the second row. The X's indicate the ESNIS if areas outside the reserve network are uninhabitable, and circles indicate the ESNIS if constant-effort harvest occurs outside reserves. See table 1 for parameter values.

retention within reserves $R(s_0^i)$ in terms of the dispersal kernel, dispersal (larval size) strategy, and reserve network design.

In box 1, we define the fecundity ($N(s_0)$), survival ($L(s_0)$), and retention ($R(s_0)$) as functions of initial larval size. As stated above, we assume there is a trade-off between fecundity and initial larval size, where $N(s_0)$ is a monotonically decreasing function of s_0. In addition, we consider two possibilities for the larval survival: (1) differential mortality in the benthic and pelagic stages and (2) size-dependent mortality. In the next sections, we present analytical and numerical explorations of the basic model (eqq. [1]–[3]) for the two approaches described in box 1 (eqq. [4]–[8]).

Case 1 Analytic Exploration. To determine the initial larval size s_0^* that maximizes $F(s_0)$ (eq. [3]), we first take the derivative of $\ln(F(s_0))$:

$$\frac{d\ln(F(s_0))}{ds_0} = \frac{d\ln(N(s_0))}{ds_0} + \frac{d\ln(L(s_0))}{ds_0} + \frac{d\ln(R(s_0))}{ds_0}. \tag{9}$$

Then, for each model, we separate the positive and negative components of $d\ln(F(s_0))/ds_0$; the absolute value of the negative component (G_-) relative to the positive component (G_+) indicates whether fitness is increasing ($G_+ > G_-$, or $d\ln(F(s_0))/ds_0 > 0$), decreasing ($G_- > G_+$, or $d\ln(F(s_0))/ds_0 < 0$), or at a minimum or maximum ($G_- = G_+$, or $d\ln(F(s_0))/ds_0 = 0$). Based on the functional forms of G_+ and G_- in a pristine environment, we qualitatively explore all possible scenarios for the relative values of G_+ and G_- over the biologically relevant range

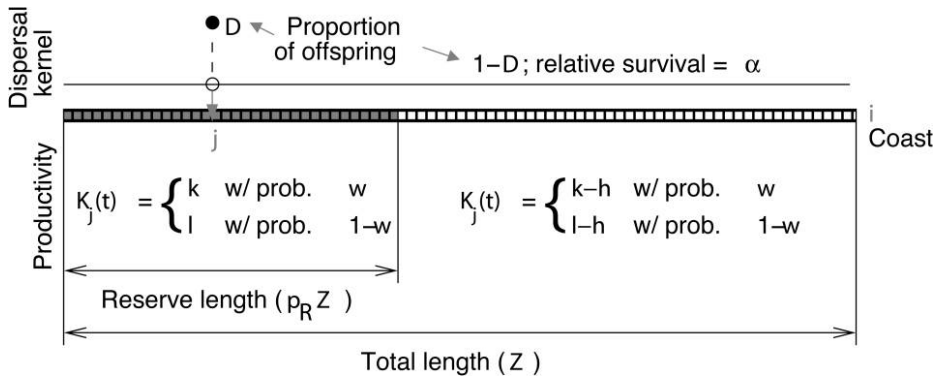

Figure 6: Outline of the case 2 (unpredictable variation) model, where temporal heterogeneity is the primary selective force acting on the evolution of dispersal (eq. [11]). See text for definition of terms.

of initial larval sizes $s_{\min} \le s_0 \le s_{\max}$. This comparison indicates the potential value of s_0^* that maximizes $F(s_0)$ and therefore is the stable strategy before habitat fragmentation. Finally, we determine the impact of adding fragmentation into a reserve network on the fitness-derivative components and thus the stable strategy s_0^*.

For the analytical exploration, we make no assumptions about the shape of the dispersal kernel (double exponential, normal, etc.). Instead, we assume two general properties for larval retention within a reserve network $R(s_0)$. First, we assume dispersal distance decreases with increasing initial larval size s_0, which means increased probability that a larvae initially released in a reserve network stays within the reserve network; thus, $R(s_0)$ is an increasing function of s_0, or $d\ln(R(s_0))/ds_0 > 0$. Second, we assume that in the pristine state, or when the entire coastline is protected ($r_w = 1$), $R(s_0) = 1$. Both of the above assumptions hold for the double exponential dispersal kernel used in equation (8) and the numerical analysis in "Case 1 Numerical Exploration."

Differential mortality model analysis. First we analyze the approach with differential mortality in the benthic and pelagic stages. In appendix A, available in the online edition of the *American Naturalist*, we calculate the fitness derivative (eq. [9]) given the survival and fecundity functions in equations (4) and (5), respectively, and we separate the positive (G_+; eq. [A2]) and negative (G_-; eq. [A3]) components of the fitness derivative. Given the assumption that the retention derivative $d\ln(R(s_0))/ds_0 > 0$ in a reserve network, fragmentation into a reserve network increases the value of G_+. Based on this fact and the functional forms of G_+ and G_- in a pristine environment ($r_w = 1$ and $d\ln(R(s_0))/ds_0 = 0$), there are four possible scenarios for the larval strategy s_0^* that maximizes fitness and the effect of fragmentation (fig. 2), detailed below.

First, in some parameter space when the maximum total pelagic mortality is greater than the maximum total benthic mortality ($\delta_p p > \delta_l l$), an intermediate (mixed benthic and pelagic) larval strategy s_0^* may maximize the fitness. In this case, the value of s_0^* that maximizes fitness increases with fragmentation into a reserve network (fig. 2*A*). Therefore, fragmentation shifts the stable strategy toward reduced dispersal by decreasing the time in the pelagic stage that maximizes fitness.

Second, in the remaining parameter space when $\delta_p p > \delta_l l$, the larval strategy that maximizes fitness is $s_0^* = s_{\max}$. This parameter space increases with fragmentation into a reserve network (fig. 2*B*). Therefore, fragmentation shifts the stable strategy toward reduced dispersal by increasing the parameter space where none of the larval period in the pelagic stage maximizes fitness.

Third, in some parameter space when the maximum total benthic mortality is greater than the maximum total pelagic mortality ($\delta_l l > \delta_p p$), the larval strategy that maximizes fitness may be $s_0^* = s_{\min}$. This parameter space decreases and s_0^* may shift from $s_{\min}$ to local maxima at $s_{\min}$ and $s_{\max}$ with fragmentation into a reserve network (fig. 2*C*). Therefore, fragmentation shifts the stable strategy toward reduced dispersal by decreasing the parameter space where the entire larval period in the pelagic stage maximizes fitness.

Fourth, in the remaining parameter space when $\delta_l l > \delta_p p$, both $s_{\min}$ and $s_{\max}$ locally maximize fitness. This parameter space increases with fragmentation into a reserve network (fig. 2*D*). Therefore, depending on whether $s_{\max}$ globally maximizes fitness (i.e., $F(s_{\max}) > F(s_{\min})$), fragmentation has the potential to shift the stable strategy toward reduced dispersal by increasing the parameter space where none of the larval period in the pelagic stage maximizes fitness.

Note that a greater benthic than pelagic mortality is necessary for benthic predation to increase selection pres-

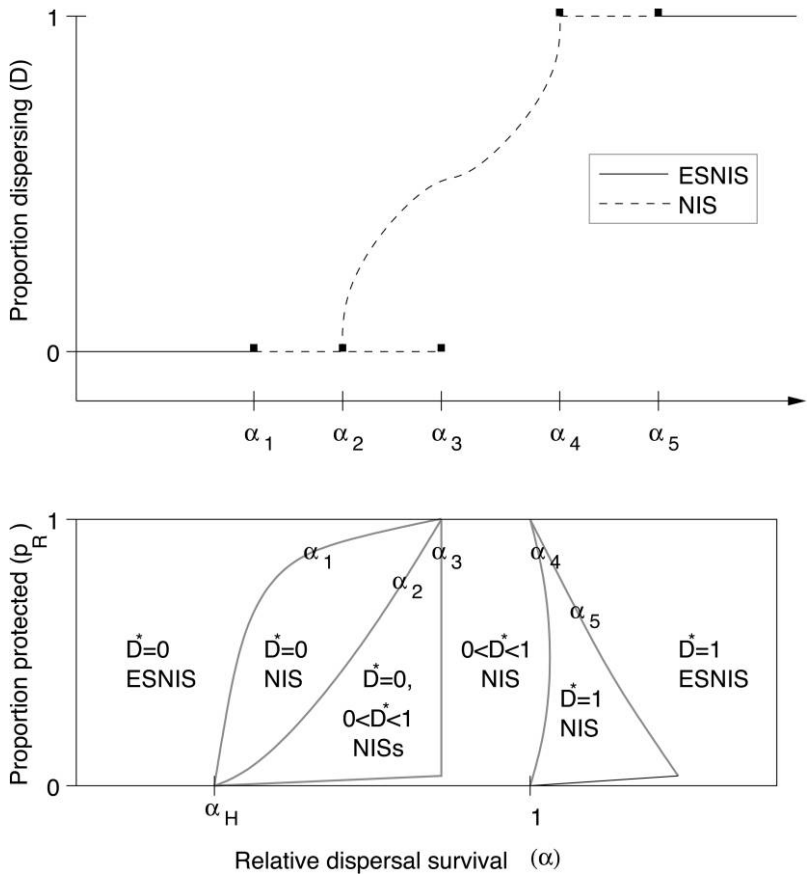

Figure 7: Potential outcomes of the case 2 (unpredictable variation) model. The top graph (adapted from Cohen and Levin's fig. 9 [1991]), indicates the global evolutionarily stable and/or neighborhood invader dispersal strategies as a function of the relative dispersal survival in an environment with two types of habitat. The bottom plot indicates the parameter space for these outcomes depending on the values for relative dispersal survival and proportion protected in a network of reserves surrounded by constant-quota harvested areas. NIS = neighborhood invader strategy; ESNIS = evolutionarily stable neighborhood invader strategy.

sure for planktonic dispersal; if the pelagic mortality is greater, the primary selective force promoting planktonic dispersal is the offspring size-number trade-off and therefore the existence of a pelagic feeding period. In all of the above scenarios, fragmentation into a reserve network shifts the stable strategy toward reduced dispersal.

Size-dependent mortality model analysis. Second, we analyze the approach with size-dependent larval mortality. In appendix A, we calculate the fitness derivative (eq. [9]) given the survival and fecundity functions in equations (6) and (7), respectively, and we separate the positive (G_+; eq. [A5]) and negative (G_-; eq. [A6]) components of the fitness derivative. As above, fragmentation into a reserve network increases the value of G_+. Based on this fact and the functional forms of G_+ and G_- in a pristine environment, there are three possible scenarios for the larval strategy s_0^* that maximizes fitness and the effect of fragmentation (fig. 3), detailed below.

First, for a high growth rate or low mortality rate(s), an intermediate larval strategy s_0^* ($s_{\min} < s_0^* < s_{\max}$) maximizes fitness. In this case, the value of s_0^* that maximizes fitness increases with fragmentation into a reserve network (fig. 3*A*). Therefore, fragmentation shifts the stable strategy toward reduced dispersal by decreasing the pelagic duration that maximizes fitness.

Second, for intermediate growth and mortality rates, both an intermediate larval strategy and $s_{\max}$ locally maximize fitness. In this case, the value of the intermediate s_0 that locally maximizes fitness increases with fragmentation into a reserve network (fig. 3*B*). Therefore, fragmentation may shift the stable strategy toward reduced dispersal by decreasing the pelagic duration that maximizes fitness.

Third, for a low growth rate or high mortality rate(s), $s_0^* = s_{\max}$ maximizes the fitness. This parameter space increases with fragmentation into a reserve network (fig. 3*C*).

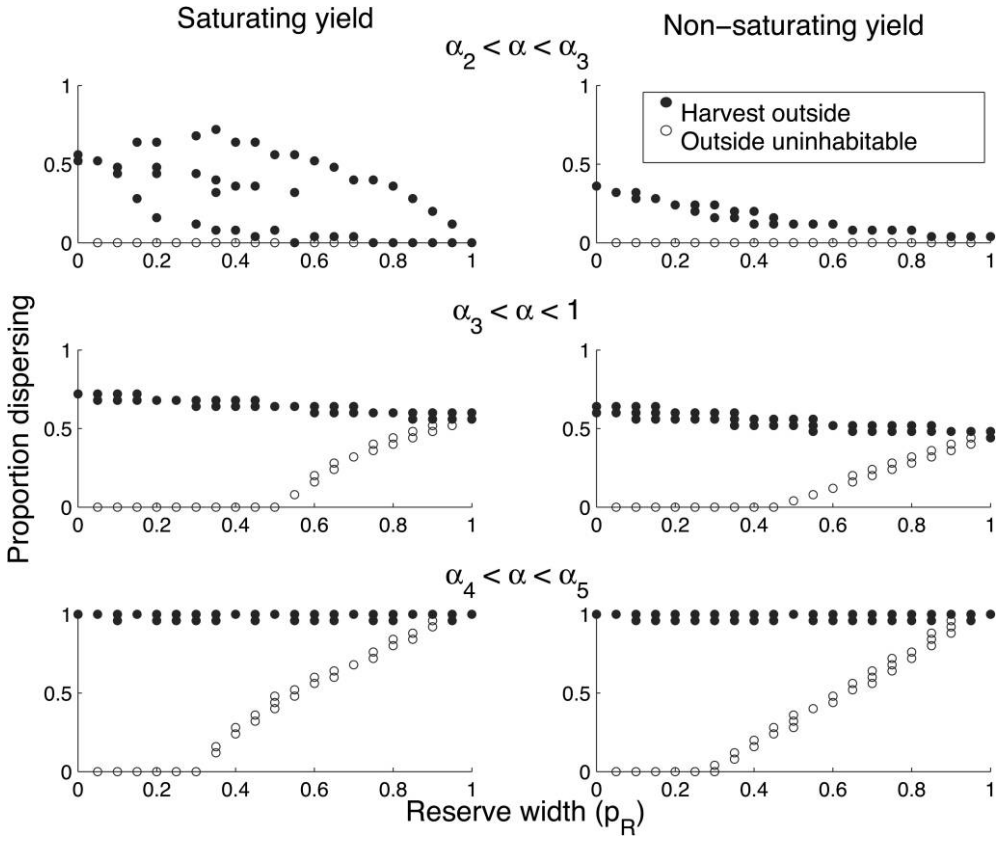

Figure 8: Numerically determined dispersal strategies or coalitions of strategies (proportion of propagules dispersing) that can invade all others and cannot be invaded for the case 2 (unpredictable variation) model with global dispersal (eq. [11]), depending on reserve width (proportion of the region protected) and model assumptions. The assumption that areas outside reserves are harvested or uninhabitable is represented in filled or open circles, respectively. The assumption of saturating or nonsaturating reproductive yield is in the left-hand or right-hand column, respectively. Differing relative dispersal survivals α, representative of the different potential outcomes from figure 7, are in each row. See table 2 for parameter values.

Therefore, fragmentation shifts the stable strategy toward reduced dispersal by increasing the parameter space where the minimum pelagic duration maximizes fitness. As with the first model, fragmentation into a reserve network shifts the stable strategy toward reduced dispersal in all of the above scenarios.

Selection strength. To determine the effect of fragmentation into a reserve network on selection strength, we explore how rapidly the fitness changes with dispersal strategy using the second derivative of the log of the fitness, calculated in appendix A. In both of the above models, if the second derivative of the within-reserve retention is nonzero, the second derivative of the fitness function changes with the fragmentation of an environment into a reserve network (eqq. [A7], [A8]). A reasonable expectation is that $d^2 \ln (R(s_0))/ds_0^2 > 0$ or the rate of increase of retention $R(s_0)$ with s_0 increases with increasing s_0. In other words, the difference in retention for two shorter-distance dispersers is greater than the difference in retention for two longer-distance dispersers with the same difference in initial larval size. Therefore, fragmentation into a reserve network has the potential to alter the absolute rate of change of fitness ($|d^2 \ln (F(s_0))/ds_0^2|$) and thus to change the selection strength.

Case 1 Numerical Exploration. To illustrate the analytical results, we provide a numerical example of the fitness function $F(s_0)$ (eq. [3]) given realistic parameter values and the reserve retention function $R(s_0)$ in equation (8). Furthermore, we use numerical simulations to explore the effects of frequency dependence, edge effects, and the assumption that areas outside the reserve are uninhabitable, which we could not examine analytically.

In the numerical simulations, we discretize space and follow the number of individuals $n_{x,t}(s_0^i)$ with larval strategy s_0^i at location x and time t. The dynamics in the larval stage follow the survival ($L(s_0)$) and fecundity ($N(s_0)$) functions defined above (eqq. [4], [5] or [6], [7]). To

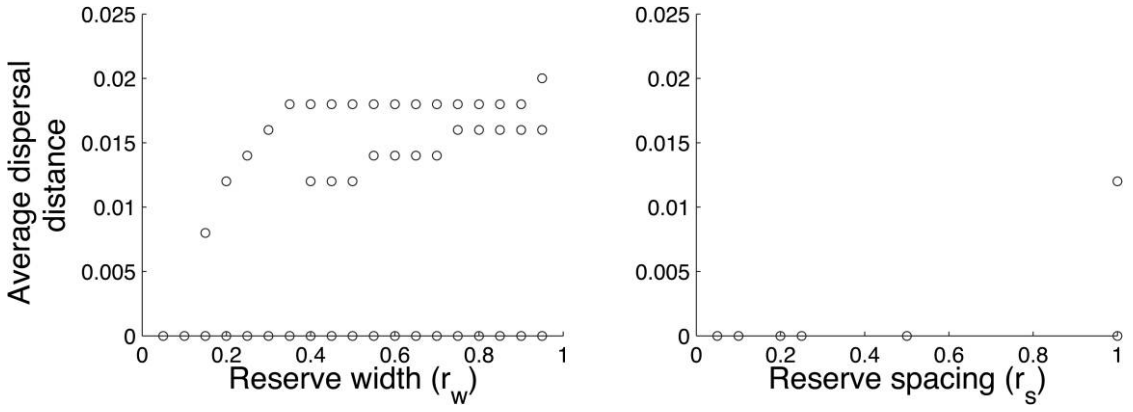

Figure 9: Numerically determined dispersal strategies or coalitions of strategies (average dispersal distance relative to the region length) that can invade all others and cannot be invaded for the case 2 (unpredictable variation) model with localized dispersal (eq. [12]), depending on reserve width (proportion of the region protected in one reserve) or spacing (proportion of the region with 20% protected in total). See table 2 for parameter values. In the simulations, areas outside reserves are uninhabitable and the reproductive yield is nonsaturating.

account for the postsettlement stage, the postlarval survival probability V_x depends on location x. If the areas outside reserves are uninhabitable, $V_x = v$ for x in reserves and $V_x = 0$ for x outside reserves. We compare this to the case with reduced survival due to constant-effort harvest, or $V_x = hw$, where $0 < h < 1$, for x outside reserves.

For the dispersal dynamics, as a discrete analog to the double exponential distribution used in equation (8), we use a double gamma dispersal kernel $\kappa_{x,y}(s_0^i) = (1 - A(s_0^i))^{|x-y|}A(s_0^i)/2$ given release location y, settlement location x, and mean dispersal distance $(1 - A)/A$. Given the relationship between mean dispersal distance and planktonic larval duration described above, the dispersal parameter is $A(s_0^i) = (1 + T_L(s_0^i))^{(-1/q)}$.

Given the above definitions, we numerically iterate the spatially discrete version of equation (1),

$$n_{x,t+1}(s_0^i) = \sum_{y=1}^{Z} \kappa_{x,y}(s_0^i)L(s_0^i)N(s_0^i)V_y\frac{n_{y,t}(s_0^i)}{\sum_j n_{y,t}(s_0^j)}, \quad (10)$$

for all possible pairs of invading and dominant strategies. By fitting the invading strategy time series to an exponential curve, we determine invasion success (positive growth) or failure (negative growth). This approach allows determination of uninvadable strategies (ESSs), strategies that can invade all other strategies (NISs), and thus ESNISs.

For the spatial dynamics, we simulate the populations on a one-dimensional torus of $Z = 100$ sites (e.g., see Palumbi 2003), and we initiate each simulation with 99% of the population as the resident strategy and 1% as the invading strategy in each deme. For all numerical analyses (simulations and example fitness functions), we chose parameter values within the biologically reasonable ranges for marine invertebrates based on the values in Strathmann (1985), Rumrill (1990), and Shanks et al. (2003; table 1).

Differential mortality model numerical analysis. First we present the results for the approach with differential benthic and pelagic mortality (survival and fecundity in eqq. [4], [5]). In the numerical example of the fitness function (eq. [3]), decreasing reserve size and increasing reserve spacing (decreased reserve network fragmentation) cause the global ESNIS to abruptly shift from an intermediate larval size to the maximum size, that is, shift toward reduced dispersal (fig. 4, *top row*). In the numerical results from simulating equation (10), the predicted shifts in the global ESNIS are in the same direction but are more gradual than those predicted by the fitness function. Furthermore, the numerical results indicate that a shift in the global ESNIS toward reduced dispersal is much more likely given the assumption that areas outside reserves are uninhabitable as opposed to accounting for dynamics, with added harvest mortality, outside reserves (fig. 5, *top row*).

Size-dependent mortality model numerical analysis. Second we present the results for the approach with size-dependent larval mortality (survival and fecundity in eqq. [6], [7]). In the numerical example of the fitness function (eq. [3]), the extreme values of initial larval size s_0 ($s_{\min}$ and $s_{\max}$) locally maximize fitness (fig. 4, *bottom row*). Decreasing reserve size and increasing reserve spacing flatten the fitness curve, which suggests decreased selection strength. In both the example fitness function and the simulations of equation (10), decreasing reserve size shifts the global ESNIS toward reduced dispersal by switching the strategy that globally maximizes fitness from all ($s_0^* = s_{\min}$) to none ($s_0^* = s_{\max}$) of the larval period in the

Box 1: Definition of the survival, fecundity, and retention functions for the case 1 (predictable variation) models

Differential mortality model. To determine survival in the approach with differential mortality in the benthic and pelagic stages, we define the mortality rates in the benthic lecithotrophic and pelagic planktotrophic stages as δ_l and δ_p, respectively (similar to Vance 1973, where $\delta_l > \delta_p$ if predation avoidance in the pelagic stage is a benefit of dispersal). Let p and l be the maximum possible pelagic and benthic durations, respectively, where $p > l$. Given an initial larval size s_0 between minimum size $s_{\min}$ and maximum size $s_{\max}$, we distribute the time spent in each stage such that the relationship between larval duration and larval size matches the inverse relationship found in empirical data (Levitan 2000). Specifically, the time spent in the pelagic period is $T_L(s_0) = ps_{\min}(s_{\max} - s_0)/[(s_{\max} - s_{\min})s_0]$, analogous to Levitan (2000), and in the benthic period, it is $ls_{\max}(s_0 - s_{\min})/[(s_{\max} - s_{\min})s_0]$. Given these parameters, the larval survival $L(s_0)$ is

$$L(s_0) = \exp\left[-\frac{\delta_l l s_{\max}(s_0 - s_{\min}) + \delta_p p s_{\min}(s_{\max} - s_0)}{(s_{\max} - s_{\min})s_0}\right] \tag{4}$$

(Vance 1973; Levitan 2000). To determine the fecundity, we assume that the initial benthic larval stage requires protective encapsulation. Let the total reproductive investment be E and the larval size-dependent energetic cost per capsule be k. Then the fecundity $N(s_0)$, or the number of eggs released by a female, is

$$N(s_0) = \frac{E - ks_0}{s_0}, \tag{5}$$

analogous to the approach by Perron and Carrier (1981).

Size-dependent mortality model. To determine survival in the approach with size-dependent larval mortality, let δ_p be the baseline (size-independent) mortality and $f(s)$ be the size-dependent mortality. In addition, let $g(s)$ be the growth rate per size unit s. Then, using the standard McKendrick–von Foerster model for death in a growing population, the survival as a function of initial larval size s_0 is

$$L(s_0) = \exp\left(-\int_{s_0}^{s_{\max}} \frac{\delta_p + f(s)}{sg(s)}\,ds\right) \tag{6}$$

(Christiansen and Fenchel 1979). In the analysis below, we assume that the size-dependent mortality is a decreasing function of size s given constant c and is 0 at maximum size $s_{\max}$, as suggested by Christiansen and Fenchel (1979): $f(s) = c(s_{\max} - s)/(s_{\max}s)$ (see Rumrill 1990 for a review of the empirical evidence in support of decreased larval predation with age, and therefore, given growth, size). In addition, we assume sigmoidal growth with constants α and β and maximum size $s_{\max}$: $g(s) = \alpha[(s_{\max} + \beta) - s]/(s_{\max} + \beta)$ (Christiansen and Fenchel 1979). Note that the relationship between initial larval size s_0 and time spent in the pelagic larval period $T_L(s_0) = \int_{s_0}^{s_{\max}} (sg(s))^{-1} ds$ is similar to but not exactly the relationship used above that Levitan (2000) proposes from empirical data. To determine the fecundity, we assume no initial benthic stage and therefore no encapsulation costs. Thus, the fecundity is the total reproductive investment E divided by the initial larval size

$$N(s_0) = \frac{E}{s_0} \tag{7}$$

(Christiansen and Fenchel 1979).

Retention. In both approaches, retention within a reserve network $R(s_0)$ is the integral of a dispersal kernel, with average dispersal distance dependent on initial larval size s_0, over a reserve network with individual reserve width r_w and reserve spacing r_s (r_w plus the distance between individual reserves; fig. 1). For example, the double exponential (Laplacian; chosen for analytic tractability) dispersal kernel κ given mean dispersal distance $1/a(s_0)$, release location y, and settlement location x is $\kappa(x, y, s_0) = (a(s_0)/2)\exp(-a(s_0)|x - y|)$. Then, given the assumption of an infinite linear coastline, the average proportion of larvae produced in a reserve network that settle in that reserve network is

$$R(s_0) = \frac{(e^{a(s_0)r_w} - 1)(1 - e^{-a(s_0)r_w})e^{-a(s_0)r_s}}{a(s_0)r_w(1 - e^{-a(s_0)r_s})} + 1 - \frac{1 - e^{-a(s_0)r_w}}{a(s_0)r_w} \tag{8}$$

(Van Kirk and Lewis 1997; Botsford et al. 2001). Given the linear relationship between the log of the mean dispersal distance $1/a$ and the log of the planktonic larval duration $T_L(s_0)$ (Shanks et al. 2003), let $a(s_0) = (T_L(s_0))^{-1/q}$, where q is a constant.

Table 1: Parameter values used in the numerical analysis of the predictable variation models (fig. 1; eqq. [1]–[10])

	Description	Value(s)
Parameters:		
s_0	Initial larval size	$s_{min} - s_{max}$
s_{min}	Minimum larval size	50 μm
s_{max}	Maximum larval size	1,000 μm
E	Total reproductive investment	10^7, 10^4 energy units[a]
δ_p	Size-independent pelagic larval mortality	.2 day^{-1}
ν	Postlarval survival	.5
h	Harvest survival	0, .5
q	Dispersal distance/pelagic larval duration exponent	.8
r_w	Reserve width	0–1
r_s	Reserve spacing	0–1
Additional parameters for the differential mortality model:		
δ_l	Benthic larval mortality	.3 day^{-1}
p	Maximum pelagic duration	70 days
l	Maximum benthic duration	30 days
k	Energetic investment per capsule	.3 E/s_{max}
Additional parameters for the size-dependent mortality model:		
α	Sigmoidal growth constant	.5 day^{-1}
β	Sigmoidal growth constant	10 μm
c	Size-dependent mortality constant	.1 day^{-1}

Sources: Strathmann 1985; Rumrill 1990; Levitan 2000; Shanks et al. 2003.

[a] Because E affects absolute but not relative fitness, we adjust E such that the absolute fitness falls within a biologically reasonable range, where $E = 10^7$ energy units (total mass, converted to length, of larvae that can be produced) in the differential mortality model and $E = 10^4$ energy units in the size-based mortality model.

pelagic stage (figs. 4, 5, *bottom rows*). As above, in the simulations, shifts in the global ESNIS toward reduced dispersal with reserve network establishment are much more likely given the assumption that areas outside reserves are uninhabitable as opposed to harvested.

Case 2: Unpredictable Variation and the Evolution of Proportion of Offspring Dispersing

Previous explorations of the evolution of dispersal in temporally heterogeneous habitats have explored a variety of approaches (e.g., genotypic or phenotypic), sources of temporal heterogeneity (stochastic reproductive yield, patch extinction, etc.), and spatial dynamics (reviewed by Johnson and Gaines [1990]). Here we use a phenotypic, game-theoretic approach where temporal heterogeneity in productivity is the primary selective force acting on dispersal in a pristine environment.

Case 2 Model Definition. To start with the simplest possible approach, we modify the model of Cohen and Levin (1991) with two habitat types, which is analogous to having no-take reserves and harvested areas. In their model, $S_i^D(t)$ is the number of propagules with strategy D in site i at time t, $Y_i(t)$ is the reproductive yield in site i at time t, D is the fraction of propagules that disperse globally (with $1 - D$ of the propagules remaining in site i), α is the survival for dispersing propagules relative to nondispersing propagules, and Z is the length (number of sites) of the region. Then the following iteration describes the dynamics:

$$S_i^D(t+1) = S_i^D(t)Y_i(t)(1-D) + \frac{\alpha D}{Z}\sum_{j=1}^{Z} S_j^D(t)Y_j(t) \quad (11)$$

(Levin et al. 1984; Cohen and Levin 1991). Given productivity $K_j(t)$ and saturating reproductive yield, $Y_j(t) = K_j(t)/\sum_D S_j^D(t)$; one example of nonsaturating yield given constant b is $Y_j(t) = K_j(t)/(\sum_D S_j^D(t) + b)$ (Levin et al. 1984; Cohen and Levin 1991). To represent good and bad years, $K_j(t)$ can take on one of two values in each habitat type. To apply this model to the case of reserves and harvested areas, $K_j(t)$ is reduced by the constant take (quota) harvest h for j outside the no-take reserve network that protects proportion p_R of the habitat. Therefore, $K_j(t) = k_j$ with probability w, and $K_j(t) = l_j$ with probability $1 - w$, where

$k_j = k$ and $l_j = l$ for j in reserves and $k_j = k - h$ and $l_j = l - h$ for j in harvested areas (for $h < k, l$; fig. 6).

Case 2 Analytic Exploration. Cohen and Levin (1991) analytically determine the evolutionary optimal dispersal strategies for equation (11) given saturating reproductive yield and the general case of two types of habitat. In appendix B, available in the online edition of the *American Naturalist*, we summarize their analysis and apply it to the specific case of reserves and constant-quota harvested areas. The results indicate that the evolutionarily optimal strategy depends on the relative dispersal survival α compared to the five successive values $\alpha_1 < \alpha_2 < \alpha_3 < \alpha_4 < \alpha_5$ defined in equations (B17)–(B21). In particular, (1) if $\alpha < \alpha_1$, $D^* = 0$ (no offspring dispersing) is a global ESNIS; (2) if $\alpha_1 < \alpha < \alpha_2$, $D^* = 0$ is a global NIS but not an ESS; (3) if $\alpha_2 < \alpha < \alpha_3$, $D^* = 0$ and an intermediate D^* $(0 < D^* < 1)$ are both global NISs; (4) if $\alpha_3 < \alpha < \alpha_4$, an intermediate D^* is a global NIS; (5) if $\alpha_4 < \alpha < \alpha_5$, $D^* = 1$ (all offspring dispersing) is a global NIS and local ESS; and (6) if $\alpha > \alpha_5$, $D^* = 1$ is a global ESNIS. If the entire coastline is harvested (no reserves; $p_R = 0$), $\alpha_1 = \alpha_2 = \alpha_3 = \alpha_H$, where α_H is defined in equation (B22). To determine the effect of reserve design on the evolutionary optimal dispersal strategies, we explore how the reserve width p_R affects the threshold dispersal survivals α_i (fig. 7).

Fragmentation into a reserve network has the potential to alter the evolution of dispersal if $\alpha_H < \alpha < \alpha_5$. If dispersal survival is low $(\alpha_H < \alpha < \alpha_3)$, decreasing protection in a reserve decreases the space in which zero dispersal $(D^* = 0)$ is a global ESNIS (as opposed to a non-ESS NIS; fig. 7). This occurs because decreasing protection increases the average ratio of productivity in good years to bad years $([k - h] : [l - h] > k : l)$ and thus the stochastic environmental variability that makes dispersal advantageous. In this case, fragmentation into a reserve network may shift the predicted evolutionary outcome toward less dispersal compared to an entirely disturbed state $(p_R = 0)$ and shift the predicted evolutionary outcome toward more dispersal compared to a pristine, or entirely protected, state $(p_R = 1)$.

In addition, if retention has lower survival than dispersal $(1 < \alpha < \alpha_5)$, establishing a reserve network in a harvested region initially decreases the parameter space in which 100% dispersal $(D^* = 1)$ is a global ESNIS (compared to a local ESS and global NIS), but then that parameter space increases with increasing protection (fig. 7). Here the predicted evolutionary outcome depends on the trade-off between the disadvantage of moving from an unfavorable to a favorable habitat and the survival benefit from dispersal. In this case, decreasing protection may shift the predicted evolutionary outcome toward less dispersal compared to both the pristine state $(p_R = 1)$ and the fully disturbed state $(p_R = 0)$.

Overall, for $\alpha_H < \alpha < \alpha_5$, the fragmentation of a habitat into a reserve network surrounded by harvested areas introduces previously nonexistent neighborhood invader dispersal strategies that are not ESNISs. Such non-ESS NISs create the opportunity for combinations of coexisting types to be the predicted evolutionarily outcome (Ludwig and Levin 1991) and may represent branching points (Mathias et al. 2001). While the parameter space where these outcomes may occur decreases with increasing protection, this result suggests that fragmentation into a reserve network may result in increased variability in the evolution of dispersal.

These predicted shifts rely on the assumption of constant-quota harvest. If constant-effort harvest occurs outside reserves, productivities $k_j = fk$ and $l_j = fl$ for j in harvested areas given $0 < f < 1$. Then the average ratio of productivity in good years to bad years is the same in harvested areas $(fk : fl)$ as in reserves $(k : l)$. In this case, the threshold dispersal survival values α_1 and α_3 from equations (B12) and (B14) are equivalent and independent of the proportion of habitat-protected p_R. Thus the reserve size does not change the evolutionarily optimal dispersal strategy for any relative dispersal survival $\alpha < 1$.

Case 2 Numerical Exploration. To explore the potential for coalitions of strategies to be the predicted evolutionary outcome in a reserve network with constant-quota harvest outside reserves, we numerically analyze equation (11). As with the case 1 (predictable variation) models, we numerically iterate the model with all possible pairs of invading and dominant strategies, and then we fit the invading strategy time series to an exponential growth curve to determine invasion success or failure. Given the stochastic nature (temporal heterogeneity) of the simulations, we determine the median and 95% confidence interval of the exponential growth rate from repeated simulations. If there is no single strategy that is a global ESNIS, we search for coalitions of strategies, starting with coalitions of two and increasing the coalition size up to five, composed of mutually invasible strategies that together can invade all strategies and cannot be invaded by any other strategies.

For the numerical simulations, we use parameter values similar to those in Ludwig and Levin (1991) and table 2. We use $Z = 100$ sites and 20 time steps for each invasion attempt; we simulate 100 invasion attempts for each invasive-dominant pair and initiate each population with 99% of the resident strategy(ies) and 1% of the invading strategy at each deme. As with the previous models, we compare the simulations with constant-quota harvest (productivities $k_j = k - h$ and $l_j = l - h$ for j in harvested areas) to simulations where areas outside the reserve are

Table 2: Parameter values used in the numerical analysis of the unpredictable variation models (fig. 6; eqq. [11], [12])

	Description	Value(s)
Parameter:		
D	Proportion of offspring dispersing	0–1
k	Reproductive yield in a good year	100
l	Reproductive yield in a bad year	10[a]
h	Constant-effort harvest	$.9 \times \min(k, l)$[b]
w	Probability of a good year	.5
b	Nonsaturating yield constant	0, 10
p_R, r_w	Reserve width	0–1
Additional parameters for the global dispersal model:		
α	Relative dispersal survival	Constant-quota harvest: .3257, .6653, 1.0048 Outside uninhabitable: .3393, .6653, 1.0526
Additional parameters for the localized dispersal model:		
δ	Dispersal mortality	.125 days^{-1}
q	Dispersal distance/pelagic larval duration exponent	.78
r_s	Reserve spacing	0–1

Sources: Rumrill 1990; Ludwig and Levin 1991; Shanks et al. 2003.

[a] That is, 10 : 1 productivity ratio in good : bad years in reserves.

[b] That is, 91 : 1 productivity ratio in good : bad years in harvested areas.

uninhabitable; that is, $k_j = l_j = 0$ for j in harvested areas. Note that the constant-quota harvest used here differs from the constant-effort harvest used in the case 1 numerical simulations. Also, the dichotomy of remaining in place or dispersing globally (rather than having a dispersal kernel) causes dispersing propagules to be unaffected by any changes in reserve spacing for a constant total area protected. Therefore, we explore only changes in reserve size and not reserve spacing.

In the numerical simulations, the effect of fragmentation on the evolution of dispersal depends on the dynamics outside reserves (fig. 8). If areas outside reserves are uninhabitable, the habitat loss with decreasing reserve width causes the predicted evolutionary outcome to shift to a smaller proportion of offspring dispersing (especially for intermediate and large relative dispersal survival α; fig. 8, *open circles*). Alternatively, if areas outside reserves have lower productivity due to constant-quota harvest, the increase in the average productivity ratio of good to bad years with decreasing reserve width causes the predicted evolutionary outcome to shift to a greater proportion of offspring dispersing (especially for small and intermediate relative dispersal survival α; fig. 8, *filled circles*). Furthermore, the establishment of a reserve network ($0 < p_R < 1$) can result in previously nonexistent, wide-ranging coalitions of dispersal strategies to be the predicted evolutionary outcome (particularly in the case with harvest outside reserves, saturating reproductive yield, and small relative dispersal survival; fig. 8, *top left*; note that, due to computational limitations, these results do not include any coalitions of more than five strategies).

Finally, to test the impact of localized dispersal, we present a preliminary exploration of simulations with a dispersal kernel rather than global dispersal. Analogous to the case 1 (predictable variation) models, we use the double gamma dispersal kernel $\kappa_{i,j}(D) = (1 - D)^{|i-j|}D/2$ given release site j, settlement site i, and mean dispersal distance $(1 - D)/D$. Also analogous to the case 1 models, the average dispersal duration $[(1 - D)/D]^q$ depends on the mean dispersal distance and the constant q based on the empirical relationship described by Shanks et al. (2003). Let δ be the mortality rate in the dispersal stage. As defined above for the global dispersal approach, $S_i^D(t)$ is the number of propagules in location i at time t for dispersal strategy D, Z is the number of sites, and $Y_i(t)$ is reproductive yield. Then the simulations follow the iteration

$$S_i^D(t + 1) = e^{-\delta[(1-D)/D]^q} \sum_{j=1}^{Z} Y_j(t)\kappa_{i,j}(D)S_j^D(t). \qquad (12)$$

As described above, we simulate equation (12) for combinations of resident and invading strategies to determine the ESNISs (simulations on a torus with parameter values

in table 2). Because the model uses a dispersal kernel, we explore the ESNISs both for varying individual reserve width r_w and reserve spacing r_s (r_w plus distance between reserves) in a reserve network. Preliminary numerical results indicate that coalitions of strategies are a possible evolutionary outcome, even with nonsaturating reproductive yield and when areas outside reserves are uninhabitable (fig. 9; note that wide-ranging coalitions were not a predicted evolutionary outcome under these assumptions in the global dispersal approach). In this case, decreasing reserve width and reserve spacing (increasing reserve network fragmentation) both lead to a decrease in the predicted average dispersal distance(s) (fig. 9).

Discussion

The fragmentation of an environment into a reserve network generally shifts the predicted evolutionary outcomes toward reduced dispersal in the models presented here, depending on the selective forces acting on dispersal and the dynamics outside reserves. In the predictable variation models, where dispersal evolves as an adaptation to avoid benthic predation and/or feed pelagically through a planktonic stage, retention within a reserve network, and therefore survival, decreases with increasing dispersal distance in a fragmented environment. As a result, fragmentation into a reserve network shifts the global ESNISs (see "Model Overview" for a detailed explanation of this concept) toward reduced dispersal distance through (1) increased selection pressure for short-distance dispersal, (2) reduced selection pressure for long-distance dispersal, and (3) a shift in selection pressure toward reduced dispersal when intermediate dispersal distances are possible (figs. 2, 3).

Intuitively, smaller reserve networks have a greater impact on the predicted evolutionary outcomes (fig. 4), and greater anthropogenic impacts outside reserves result in greater changes in the evolutionarily predicted dispersal distance (fig. 5). Extremely fragmented reserve networks have the potential to shift selection pressure toward increased dispersal distance (figs. 4, 5), possibly because in such networks, individual reserves are too small to support populations without increased connectivity through dispersal; similar results of a shift in selection toward increased dispersal at high levels of habitat degradation or cost to dispersal occur in models with patch extinction (Comins et al. 1980; Gandon and Michalakis 1999; Heino and Hanski 2001). Numerical results here indicate that the predicted evolutionary outcome may change when accounting for spatial dynamics and frequency dependence (fig. 4 vs. fig. 5). However, the qualitative trend of selection pressure shifting toward reduced dispersal distance with decreasing reserve size still occurs when we assume strong impacts outside reserves. The results here under the assumption that areas outside reserves are uninhabitable are most relevant to cases with extreme overfishing or habitat destruction outside reserves.

In the unpredictable variation model, where dispersal evolves as an adaptation to stochastic environmental heterogeneity, decreased protection in reserves is equivalent to habitat loss if areas outside reserves are uninhabitable. Therefore, as above, the resulting increase in potential for leaving the suitable habitat (reserves) with increasing dispersal leads to a shift in global ESNISs toward reduced proportion of offspring dispersing with decreasing reserve size (fig. 8). However, if areas outside reserves are habitable but have reduced productivity due to constant-quota harvest, the increasing average ratio of productivity in good to bad years with decreasing reserve size shifts selection pressure toward increasing proportion of offspring dispersing in some cases (figs. 7, 8). In other words, the advantage of dispersal within harvested areas (due to increased ratio of productivity in good to bad years) outweighs the disadvantage of dispersal from reserves to harvested areas (due to increased probability of moving from a good habitat to a bad habitat). These results parallel the results from a model of butterfly metapopulation dynamics, where habitat degradation can also lead to increased or decreased dispersal rates, depending on its relative impact on patch extinction risk (the primary natural selective force acting on dispersal) and dispersal risk (Heino and Hanski 2001).

The potential for an increase in dispersal with fragmentation into a reserve network here depends on the assumption of constant-quota harvest. If constant-effort (proportional) harvest occurs outside reserves, the average ratio of productivity in good to bad years, and therefore the primary selective force on dispersal, would not change with reserve size. Furthermore, if the fishery's take is (proportionally) greater in good years than in bad years (e.g., constant-stock-size harvest strategy), selection may shift to decreased proportion of offspring dispersing with decreasing protection, as in the case where areas outside reserves are uninhabitable. While many fisheries employ constant-effort and constant-stock-size harvest strategies, some fisheries use a constant-quota strategy, as the Tasmanian abalone fishery did for several years (Hilborn and Walters 1992).

In addition to shifting the ESNISs, habitat fragmentation into a reserve network may alter the variation in dispersal strategies. In the models with predation and/or feeding as the primary selective forces, fragmentation into a reserve network alters the selection strength based on the rate of change in fitness; changes in selection strength may lead to altered genetic variation given mutation-selection balance. Furthermore, in the model with stochastic environmental heterogeneity, constant-quota har-

vest outside reserves, and low relative dispersal survival, fragmentation into a reserve network results in a shift from a single ESNIS to coalitions of strategies that together can invade all others and cannot be invaded (figs. 7, 8). Preliminary numerical results with more realistic dispersal dynamics indicate that such shifts in the predicted evolutionary outcome to coalitions of strategies may occur under more general conditions (e.g., nonsaturating as well as saturating reproductive yield; fig. 9). Possibly occurring due to the differential selection in reserves and harvested areas mentioned above (similar to Mathias et al. 2001), such shifts to coalitions indicate a potential for increased variability in dispersal strategies with habitat fragmentation.

Connecting the ESNISs to Rapid Evolutionary Changes

We use game-theoretic models here to explore evolutionary possibilities in the absence of mechanistic knowledge about the genetic determination of dispersal-related traits in marine species with planktonic larvae. Whether and on what timescale the predicted ESNISs will be realized, and thus whether the predicted changes in dispersal distance will occur, depends on the population genetics of the relevant traits, including their heritability, genetic variation, interaction, and evolutionary constraints.

Larval dispersal may evolve based on changes in a variety of morphological and behavioral traits such as initial larval size, the timing of larval release, and larval swimming behavior in terms of controlling position in the water column (Morgan 1995, 2001; Shanks 1995; Levitan 2000). While life-history traits such as dispersal tend to have (narrow-sense) heritabilities around 0.2–0.3, morphological and behavioral traits tend to have higher heritabilities, around 0.3–0.5 (Mousseau and Roff 1987). Therefore, sufficient heritability for evolutionary changes to occur may exist in the relevant traits. Heritability studies specific to marine larval dispersal are rare; the few existing studies indicate that dispersal-related traits such as egg size, planktonic period, and larval settlement selectivity are heritable (Mackay and Doyle 1978; Levin et al. 1991; Toonen and Pawlik 2001; but see Holm 1990), but variation due to environmental effects may be much greater than that due to genetic effects (Havenhand 1995). In addition, some of the shifts in global ESNISs predicted here are abrupt (e.g., figs. 2, 5), and such evolutionary changes may be unlikely for traits with small mutational steps.

Furthermore, while focusing on relative dispersal mortality, the trade-off between offspring size and number, and temporally variable productivity, the models presented here ignore additional selective forces that may impact the evolution of dispersal. Neglected for mathematical simplicity, factors such as variable planktonic food availability and variable circulation patterns may impact the realized dispersal distance as much as or beyond the factors incorporated here (Shanks 1995; Allison et al. 1998; Largier 2003; McEdward and Miner 2003). The potential for altered productivity and circulation patterns with climate change (Scavia et al. 2002) presents an additional anthropogenic impact that may cause rapid evolutionary changes in dispersal distance, similar to rapid evolutionary changes in migratory bird dispersal behavior with climate change (Bearhop et al. 2005). A greater empirical understanding of the genetic control of and factors important to realized larval dispersal would inform the formulation of more detailed, mechanistic (e.g., population genetic) models of the evolution of dispersal and allow more precise predictions of the impact of habitat fragmentation. The results presented here indicate that critical assumptions for forming accurate predictions from such mechanistic models include the dynamics outside reserves and relative importance of temporal heterogeneity.

Finally, the game-theoretic models presented here do not address whether the predicted evolutionary changes may occur on timescales relevant to conservation decisions such as reserve network design. As stated in the introduction to this article, rapid (on the timescale of decades) evolution due to anthropogenic impacts can occur in general (Palumbi 2001; Ashley et al. 2003; Stockwell et al. 2003), and rapid evolution of dispersal traits has occurred in nonmarine species (McNab 1994; Cody and Overton 1996; Phillips et al. 2006). Such rapid evolution requires strong selection due to substantial anthropogenic changes or extreme isolation in habitats such as islands. With respect to marine dispersal, planktonic development is generally more easily lost than gained because it involves extra structures for feeding and movement (Strathmann 1974; Hansen 1982). Thus the tendency for fragmentation into a reserve network to shift selection pressure toward reduced dispersal occurs in the more readily evolvable direction, and anthropogenically induced evolutionary changes may be difficult to reverse if they occur.

Given the large impact of fisheries on marine systems (Botsford et al. 1997), anthropogenic impacts strong enough to cause rapid evolutionary changes can occur outside marine reserves. For example, size-selective harvesting has resulted in rapid evolutionary changes in life-history traits such as timing of maturation (Sheridan 1995; Trippel 1995; Law 2000). Theoretical investigations suggest that reserves can protect against such harvest-based selection on life-history traits in both marine and terrestrial species (Trexler and Travis 2000; Tenhumberg et al. 2004; Baskett et al. 2005). Providing empirical support for the potential for reserve establishment to affect the population genetics of protected species, populations in marine protected areas have higher genetic diversity compared to pop-

ulations in harvested areas (Pérez-Ruzafa et al. 2006). Therefore, reserves have the potential to impact rapid evolution of life-history traits such as the changes in dispersal suggested here. However, an improved understanding of the genetic determination of planktonic larval dispersal is necessary to predict the appropriate timescale of the evolutionary effects of fragmentation into a reserve network on dispersal.

Implications for Management

An understanding of dispersal is critical to designing marine reserves and predicting reserve benefits (Allison et al. 1998). The protection of longer-distance dispersers for which individual reserves are too small to support self-sustaining populations depends on the connectivity between individual reserves in a network; therefore, scientific recommendations for reserve network design depend on target species' dispersal distances (Roberts et al. 2001*a*). For example, Shanks et al. (2003) propose sizing reserves on the scale of 4–6 km and spacing reserves on the scale of 10–20 km based on the bimodality in the distribution of larval dispersal distances. In addition, Palumbi (2004) proposes sizing reserves on the scale of adult home ranges and spacing reserves on the scale of larval dispersal distances. Along with protecting impacted species, marine reserves may benefit adjacent fisheries by increasing resilience to uncertainty in fisheries and by enhancing fisheries yield (Lauck et al. 1998; Murray et al. 1999; Roberts et al. 2001*b*, 2005), depending on the species being managed (Hilborn et al. 2004). Such fisheries benefits depend on spillover from reserves due to adult movement and/or larval dispersal and vary with movement rates (Quinn et al. 1993; Gerber et al. 2003; Gaylord et al. 2005).

The potential for marine reserves to alter the evolution of dispersal distances may change the network design criteria necessary to balance conservation goals in reserves with fisheries benefits outside reserves. In particular, any evolution toward shorter-distance dispersal and the resulting increased retention within reserves would reduce spillover from reserves to adjacent fisheries while increasing protection within reserves. However, evolution toward shorter-distance dispersal would also decrease reserve network connectivity and therefore any rescue effects that may be necessary for resilience to large-scale (natural and anthropogenic) catastrophes (Allison et al. 1998, 2003). In addition, the potential for changes in variation in dispersal distance suggests that alternate recommendations for reserve spacing may be necessary to protect longer-distance dispersers. Variable reserve spacing (e.g., Kaplan and Botsford 2005; Kaplan 2006) is one alternative analogous to the general rules based on larval dispersal mentioned above; the effect of variable reserve size and spacing on the evolution of dispersal merits future investigation. In addition, establishing larger reserve networks may be necessary given that the predicted evolutionary shifts in dispersal strategies are greatest in smaller reserves. Overall, a greater theoretical and empirical understanding of how habitat fragmentation affects the evolution of dispersal is vital to effective reserve network design.

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